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**Lek hypotheses and the location, dispersion, and size of Lesser  
Prairie Chicken leks**

**Locke, Brian Alvin, Ph.D.**

**New Mexico State University, 1992**

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LEK HYPOTHESES AND THE LOCATION, DISPERSION, AND SIZE OF  
LESSER PRAIRIE CHICKEN LEKS

BY

BRIAN ALVIN LOCKE, B.S., M.S.

A Dissertation submitted to the Graduate School  
in partial fulfillment of the requirements  
for the Degree  
Doctor of Philosophy

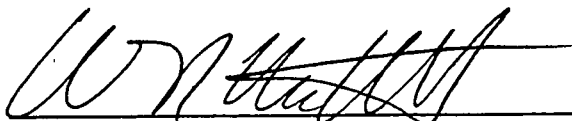
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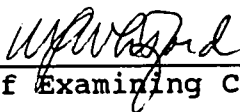
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"Lek Hypotheses and the Location, Dispersion, and Size of Lesser Prairie Chicken Leks," a dissertation prepared by Brian Alvin Locke in partial fulfillment of the requirements for the degree, Doctor of Philosophy, has been approved and accepted by the following:



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## FIELDS OF STUDY

Major Field: Biology  
Behavioral and Evolutionary Ecology

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Habitat Selection Studies  
Endangered Species

ABSTRACT

LEK HYPOTHESES AND THE LOCATION, DISPERSION, AND SIZE OF  
LESSER PRAIRIE CHICKEN LEKS

BY

BRIAN ALVIN LOCKE, B.S., M.S.

Doctor of Philosophy in Biology

New Mexico State University

Las Cruces, New Mexico, 1992

Dr. Walter G. Whitford, Chair

The location, dispersion, and size of Lesser Prairie Chicken leks in eastern New Mexico were compared with predictions of several hypothesis designed to explain lekking. Spring leks were located by driving throughout the study area and periodically stopping to listen for leks. Eighteen of 21 (85%) leks located in 1983, and 29 of 34 (85%) leks located in 1984 were located on abandoned oil well locations (oilpads).

Males did not group together to form leks because suitable display sites were limited. Failure to use some oilpads as lek sites was not related to the vegetative cover types surrounding the oilpad. Several oilpads not utilized in 1983 were utilized in 1984, thus they were

apparently suitable display sites. Furthermore, the numbers of males displaying at a lek was not related to 1) amounts of different vegetative cover types surrounding the oilpad, or 2) relative amount of vegetative cover on the oilpad itself.

Leks were too close together to be spaced in accordance with the female preference model. Most leks were closer to an adjacent lek than the one female home range diameter predicted by the female preference model. The distance at which females can detect leks would have to be between 64 to 228 m to fit the female preference model. Observations of males temporarily moving from one lek to an adjacent lek suggest prairie chickens can hear leks at least 900 m away.

Neither the least-costly male hypothesis nor the decoy/sentinel models explain the dispersion of leks. Patterns of nest locations, and new lek locations show that females do not, or can not, force leks to form in locations that will provide the proposed benefit of greater nesting success through less predation. Leks form too close to existing leks, and would attract predators into proposed zones of lower predation. Reduced nest predation may be a consequence of male group display, but not a cause.

Lesser Prairie Chicken populations tend to grow by forming new leks rather than by increasing the average

number of males per lek, a pattern consistent with the hotspot hypothesis.

Variability in the number of males attending leks, and observations of male behavior are consistent with the hotshot hypothesis.

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## INTRODUCTION

The term "lek" has been in existence since at least 1906, when it was used to describe the mating system of the Ruff (Philomachus pugnax) (Selous, in Beehler and Foster 1988). A lek is a clustered group of males that is visited by females only for the purpose of mating. A lek is a polygynous mating system in which a small proportion of males dominate in obtaining copulations (Hamerstrom and Hamerstrom 1973, Lill 1974a, Robel and Ballard 1974, Wiley 1974, Bradbury et al. 1985, Gibson and Bradbury 1986).

Bradbury (1977) suggested a set of criteria to define "classical" leks: 1) no male parental care; 2) males occupy territories that are clustered to some degree within habitat used; 3) male territories contain no resources other than the male's gametes; and 4) females have an opportunity to select a male to mate with.

The relevance of Bradbury's original criteria has changed as lekking has gained attention and investigations have occurred in different taxa (Borgia 1979, Bradbury 1985, Beehler and Foster 1988, Phillips 1990). Bradbury (1985) recognized the limitations imposed by his criteria and suggested that lack of male parental care is the primary and only strict criterion, and that his other criteria should be treated as variables. Arguments should not center on whether species actually lek or not, but on

what factors have lead to differing mating systems (Bradbury 1981, 1985). Otherwise, Bradbury (1985) argued, taxon specific definitions would need to be generated for many different situations, obscuring similarities in selective pressures operating on a variety of organisms.

Species that lek should provide good opportunities to study sexual selection because of the high variance in mating success among males on each lek, and the lack of male parental care (Bradbury and Gibson 1983, Bradbury et al. 1985). Lek mating systems provide high potential for studying intersexual selection by female choice because the males do not appear to control resources required by females for reproduction, nor do they control or defend the females directly (Emlen and Oring 1977, Bradbury and Gibson 1983). Therefore females could then be free to choose mates based on genetic quality (Gibson and Bradbury 1985).

Intrasexual selection in the form of male dominance is at least potentially important in lekking species (Diamond 1981, Avery 1984, Beehler and Foster 1988). The relative importance of inter- and intrasexual selection has been, and probably will continue to be a controversial point. Part of the differences in the explanations of how and why leks form are due to contrasting assumptions of the relative importance of inter- and intrasexual selection.

Hypotheses to explain the development of leks must propose causes for male aggregations (Bradbury 1981). Lack of male parental care is a necessary, but insufficient cause for lekking. The failure of males to help raise young does not explain why males in lekking species aggregate to form the lek. In a classification of mating systems leks can be considered only one type of system in which males are polygynous and do not provide parental care (Emlen and Oring 1977, Oring 1982).

The following review of hypotheses to explain the formation of leks closely follows the outlines of Bradbury and Gibson (1983), and Oring (1982). Hypotheses can be grouped into two general groups depending on which sex initiates the formation of the lek (Bradbury and Gibson 1983).

Males may initiate group display to maximize mating opportunities, or increase fitness by long-term survival. The hotspot hypothesis (Lill 1974a, Emlen and Oring 1977, Bradbury and Gibson 1983), hotshot hypothesis (Beehler and Foster 1988), stimulus pooling hypothesis (Snow 1963, Bradbury 1981, Oring 1982), and lack of suitable display sites (Boag and Sumanik 1969, Gullion 1976) are hypotheses to explain leks by male-initiated processes related directly to mating success.

Another possible reason for males to initiate group display is to increase lifetime fitness through survival, as opposed to increasing fitness through mating opportunities. Males may aggregate to reduce their vulnerability to predation (Hjorth 1970, Wiley 1974), or to enhance foraging success by sharing information concerning food locations (De Vos 1979).

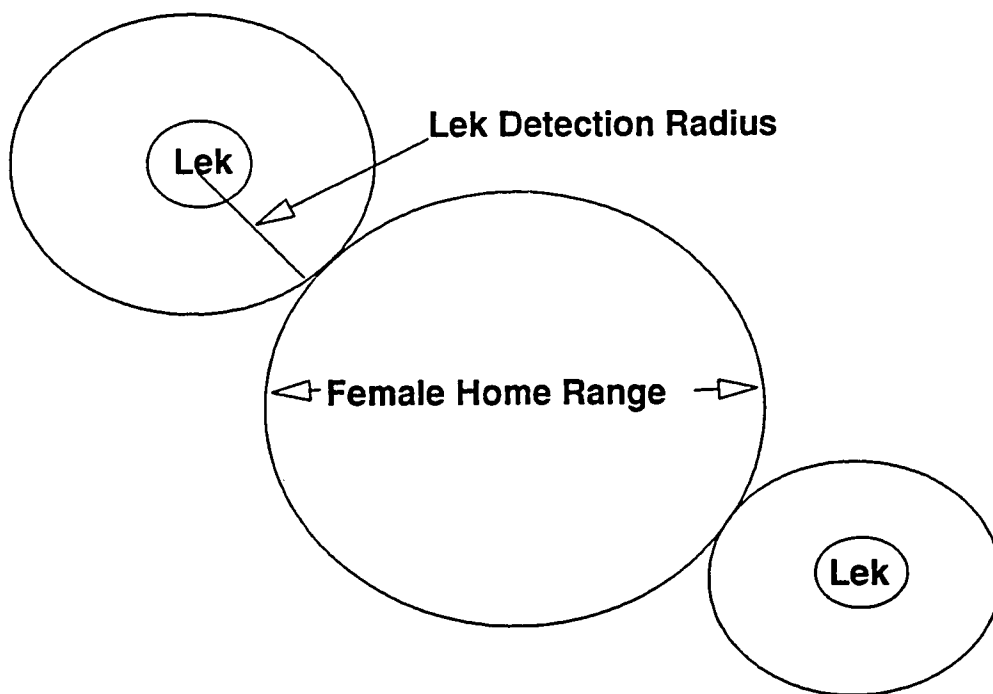
Female initiated reasons for lekking include an increased choice of males, as the female preference model suggests (Bradbury 1981), or by increasing the chance of successful nesting, which the least costly male hypothesis (Wrangham 1980) and the decoy/sentinel model (Phillips 1990) suggest.

#### **Female-Initiated Mechanisms**

The female preference model (Bradbury 1981) assumes that female preference for groups of males can essentially force leks to be farther apart than the distribution of resources needed by the males and females would require. By forcing males to aggregate, females have the opportunity to optimize mate choice (Alexander 1975, Bradbury 1981). The number of males attending a particular lek will vary, but there should be an optimal size maintained. Small leks should become extinct as females attend the larger lek to improve mate choice, and as males then abandon the smaller lek.

The female preference model predicts that leks will be spread out in such a way to maximize a female's choice of males (Bradbury 1981). Under this model females discriminate against males displaying individually, and smaller groups of displaying males, forcing all males within their home range to form one large group of displaying males. Thus the female preference model specifically predicts that adjacent leks will generally be no closer together than one female home range diameter plus the combined radii of each "active space" of the two adjacent leks. Figure 1 illustrates this prediction, called the "contiguity condition" of the female preference model (Bradbury 1981). The active space of a lek is defined as the area around the lek from which females can detect the lek (Bradbury 1981). The female preference model predicts that most females will enter only one lek active space and visit only the lek contained in that active space.

There have been few tests of the female preference model. Höglund and Robertson (1990a) report that Great Snipe (Gallinago media) lek spacing was consistent with the female preference model. Likewise, Bradbury (1981) reported that Hammer-headed Bat (Hypsignathus monstrosus) leks were spaced far enough apart to be consistent with the female preference model. Evidence



**Figure 1.** Illustration of contiguity condition of female preference model (Bradbury 1981:152).



inconsistent with the female preference model has been reported by Schroeder (1991), Svedarsky (1988), and Wegge and Rolstad (1986).

Bradbury and Gibson (1983) and Oring (1982) reviewed other hypotheses based on female initiated reasons for male clumping. One hypothesis is female choice of least costly males (Wrangham 1980, Bergerud 1988). If displaying males attract predators to nesting areas, or compete with females for foraging resources, then choosing males that are not attempting to place territories in foraging or nesting areas ("least costly males") could evolve to group display by males. Phillips (1990) pointed out that Wrangham's idea results in the prediction that nesting success should be positively correlated with the distance between nests and leks.

Evidence concerning the least costly hypothesis is conflicting. Bergerud (1988) reports that grouse nests are spaced in a manner consistent with the least costly male hypothesis, yet Phillips (1990) shows that patterns of nest success in the Greater (Tympanuchus cupido pinnatus) and Lesser Prairie Chicken (Tympanuchus cupido pallidicinctus), and the Sharp-tailed Grouse (Tympanuchus phasianellus) do not support the least-costly male hypothesis. Bradbury and Gibson (1983) and Höglund and Robertson (1990a) both present evidence that at least some lek species show large

overlaps in use of foraging space by the sexes, opposite to predictions of the least costly male hypothesis.

The decoy/sentinel model (Phillips 1990) is similar to the least costly male hypothesis, but it is based strictly on the concept that by aggregating, males at a lek may reduce predation at nests by serving as decoys, and, or sentinels. If predators were attracted to groups of displaying males then the variability in distance from leks should be less for successful nests than for unsuccessful nests (Phillips 1990).

#### **Male-Initiated Mechanisms**

Bradbury and Gibson (1983) developed the hotspot model as an alternative to the female preference model. The hotspot model suggests that the males will have more leverage in lek location than predicted by the female preference model. This model allows males to group in locations where the males will be able to display to the most females, "hotspots." The first males to settle do so at the locations near the most females, and subsequent males must choose between the best unoccupied hotspots or joining a lek at an already occupied hotspot. While the hotspot model gives the males much more leverage in determining where they will display, it assumes that males clump because of female mate choice, as does the female preference model.

The main prediction of the hotspot model is that leks should be at locations of maximal overlap of female home ranges (Bradbury and Gibson 1983, Bradbury et al. 1986). The hotspot model allows, but does not require, leks to be closer than one female home range apart. Some leks (binary leks) may be very close to adjacent ones (Bradbury and Gibson 1983). The number of males attending leks formed according to the hotspot hypothesis depends on the number of females in the vicinity of the lek.

Another male-initiated hypothesis to explain lekking is called the hotshot model (Beehler and Foster 1988). Beehler and Foster (1988) hypothesize that females do not have total control over their own choice of mate, and that inequality in mating success is produced by male-male interactions in addition to female choice. The hotshot hypothesis predicts that some males will be more successful at obtaining copulations, and less successful males will congregate around the more successful male(s), called the hotshot. If female freedom of mate choice is reduced in lek species, then secondary strategies should be observed, such as interruption of copulation attempts. This model also suggests that lek size will be variable.

Stimulus pooling is another reason males might clump to increase mating success (Snow 1963, Bradbury 1981, Oring 1982, Bradbury and Gibson 1983). Males may pool together

to attract more females than they could attract if they displayed alone (Lack 1939, Snow 1963, Hjorth 1970). Bradbury (1981) pointed out that in order for leks to evolve by this mechanism a lek must attract more females per male as the number of males at a lek gets larger. Bradbury (1981) presented a mathematical model that suggested that stimulus pooling by males is an unlikely explanation for lekking. Furthermore, field data contradict this hypothesis (Bradbury and Gibson 1983).

Lack of suitable display sites could cause males to cluster (Oring 1982, Bradbury and Gibson 1983). Boag and Sumanik (1969) showed that Ruffed Grouse (Bonasa umbellus) males displayed on logs surrounded by particular habitat. Gullion (1976) has also found habitat to be important in display site selection by Ruffed Grouse males. However, lekking males seem to use a variety of different types of sites as display sites (Anderson 1969, Taylor 1979, Connelly et al. 1981, Bradbury et al. 1989a).

Hypotheses that explain lekking by male initiated mechanisms suggest that males may enhance their lifetime fitness through survival, as opposed to the hypotheses above, which suggest the primary cause for aggregating is to increase opportunities for matings. Lifetime fitness could be enhanced by grouping to reduce predation rates on males (Wiley 1974, Wittenberger 1978), or enhancing

foraging success by exchange of information (De Vos 1979). De Vos (1979) has shown that Black Grouse (Tetrao tetrix) forage in groups and males follow other individuals to food locations. However, Oring (1982) points out that males of some altricial bird species that lek do not forage in groups, thus sharing of information about foraging areas is probably a result rather than a cause of leks.

Wiley (1974) likewise suggested that males could increase their survival by delaying reproduction their first year of life and that this delayed reproductive effort biased the operational sex ratio and allowed lekking to occur. Lewis and Jamieson (1987) present convincing evidence that yearling male Blue Grouse do indeed delay breeding. However, Wittenberger (1978) critiqued Wiley's hypothesis and noted that subadult males have been observed displaying in many species of grouse, and obtaining copulations.

Reducing vulnerability to predation has been suggested as a cause for males to display in groups (Hjorth 1970, Wiley 1974, Wittenberger 1978). However, Lill (1974b) discounts the role of predation in grouping male manakins, and Hartzler (1974) found that central males were more vulnerable to predation. Bradbury and Gibson (1983) cite a variety of studies that suggest predation is not an important factor in determining male spacing in several lek

species. Predation does not appear to be a general explanation for lekking (Oring 1982, Bradbury and Gibson 1983).

I gathered data on the location, dispersion, and sizes of Lesser Prairie Chicken leks to test several predictions of both male initiated and female initiated hypotheses concerning the nature of leks. I chose for a study area a portion of the same area used by Davis et al. (1982) to study female movements, habitat usage, and food habits of the Lesser Prairie Chicken. Many leks had already been located on study area. Dr. Charles Davis has kindly allowed me to use unpublished data gathered during his study (Davis et al. 1982).

The Lesser Prairie Chicken represents an appropriate model to test lek hypotheses against because their behaviors fit the criteria outlined by Bradbury (1977) for a "classical" lek species. Prior studies of the Lesser Prairie Chicken have focused primarily on habitat preferences and management concerns (see Candelaria 1979, Ahlborn 1980, Crawford and Stormer 1980, Cannon and Knopf 1981, Davis et al. 1981, Davis et al. 1982, Wilson 1982).

## METHODS

The study area was near Milnesand, Roosevelt County, eastern New Mexico. The study area includes the Milnesand Prairie Chicken Restoration Area, an area owned by the state of New Mexico. The area I utilized was bounded on the west by New Mexico Highway 18, and on the north by New Mexico Highway 262. I stayed west of the road that goes south from Highway 262 near the Bluitt gas plant. Leks were searched for in sections 7 through 11, 15 to 18, 19 through 22, 27 through 30, and 31 through 34 of Township 8 South and Range 36 East, and sections 11 through 14, 23 through 26, 35 and 36 of Township 8 S. Range 35 E.

Vegetation of the area was well described by Davis et al. (1982). Davis and his students recognized eight different vegetation associations on the study area. Shinnery oak (Quercus havardii) is the dominant plant in three of those habitat types: 1) shinnery oak-bluestem, 2) shinnery oak-midgrass, and 3) sandhills. With the exception of a relatively small amount of shortgrass-snakeweed, the other vegetation associations are disturbances within the shinnery-oak types. These disturbed vegetative types are termed: reverted cropland, fallow, cultivated, and weeping lovegrass (Davis et al. 1982).

The area I sampled was dominated by the three forms of shinnery oak habitat. Reverted cropland was the only disturbed vegetation of significant area, in the portion of Davis et al.'s (1982) study area in which I worked in.

Spring lek locations were determined by driving the roads, stopping periodically, and listening for leks. Searches for spring leks were conducted between 6 March and 26 April 1983, and between 13 March and 15 May 1984. Census of leks was generally done on a weekly basis. The number of birds on each lek was determined by counting, with the aid of binoculars. Only counts made early in the morning were used to determine the average number of males attending a lek. A lek was defined as a group of at least two males in attendance at a specific location at least twice during the spring.

The study area has an extensive road network resulting from oil and gas exploration. The majority of leks on the study area were located on abandoned oil well sites. These sites are commonly called "oilpads" because a clay fill is laid on top of the very sandy soil, creating a "pad", before the oil well is drilled. All oilpads, either abandoned or occupied by wells were checked for leks.

Leks were observed from either a vehicle or from blinds. A cannon net was used sparingly to capture males. In the spring of 1983 several marked males quit displaying



at lek 11. Assuming cannon netting caused the males to abandon lek 11, I made attempts to capture males with noose carpets. The noose carpets consisted of monofilament nooses attached to square pieces of "chicken wire" fencing approximately 0.3 m on each side (Anderson and Hamerstrom 1967). I sometimes used a female taxidermic mount in a copulatory position to entice males to walk on the noose carpets (Hjorth 1970). The taxidermic mount was made from a female Lesser Prairie Chicken skin obtained from hunters during the 1982 hunting season. Males captured were marked with a metal band supplied by the New Mexico Department of Game and Fish, and with colored leg bands.

I did not measure female home ranges, but instead relied on data acquired at the Prairie Chicken Restoration Area during the springs of 1979 and 1980 (Ahlborn 1980, Davis et al. 1982, Merchant 1982). Merchant (1982) used the minimum area method (Mohr 1947), and a minimum of four points to define a single home range.

All statistical tests were made using an alpha level of 0.05. Contingency tests were conducted as "R by C" tests of independence (Sokal and Rohlf 1981). Difference in means were tested with Student's t-test. Pearson's product-moment correlation was used to test for significant correlations between numbers of males on leks and amounts of different vegetative cover types within a 122 ha circle

centered on each lek. Spearman's rank correlation was used to determine if the relative amounts of vegetative cover on an oilpad was related to the number of males displaying on that pad.

## RESULTS

A total of 48 leks have been identified at the Milnesand area since 1979. Figure 2 shows the location of the leks relative to the town of Milnesand, New Mexico. Leks numbered 1 through 30 were identified during work conducted by Dr. Charles Davis and students, of the Fisheries and Wildlife Department of NMSU (Davis et al. 1982). All the leks except numbers 24, 34, and 35 occurred on abandoned oil well locations.

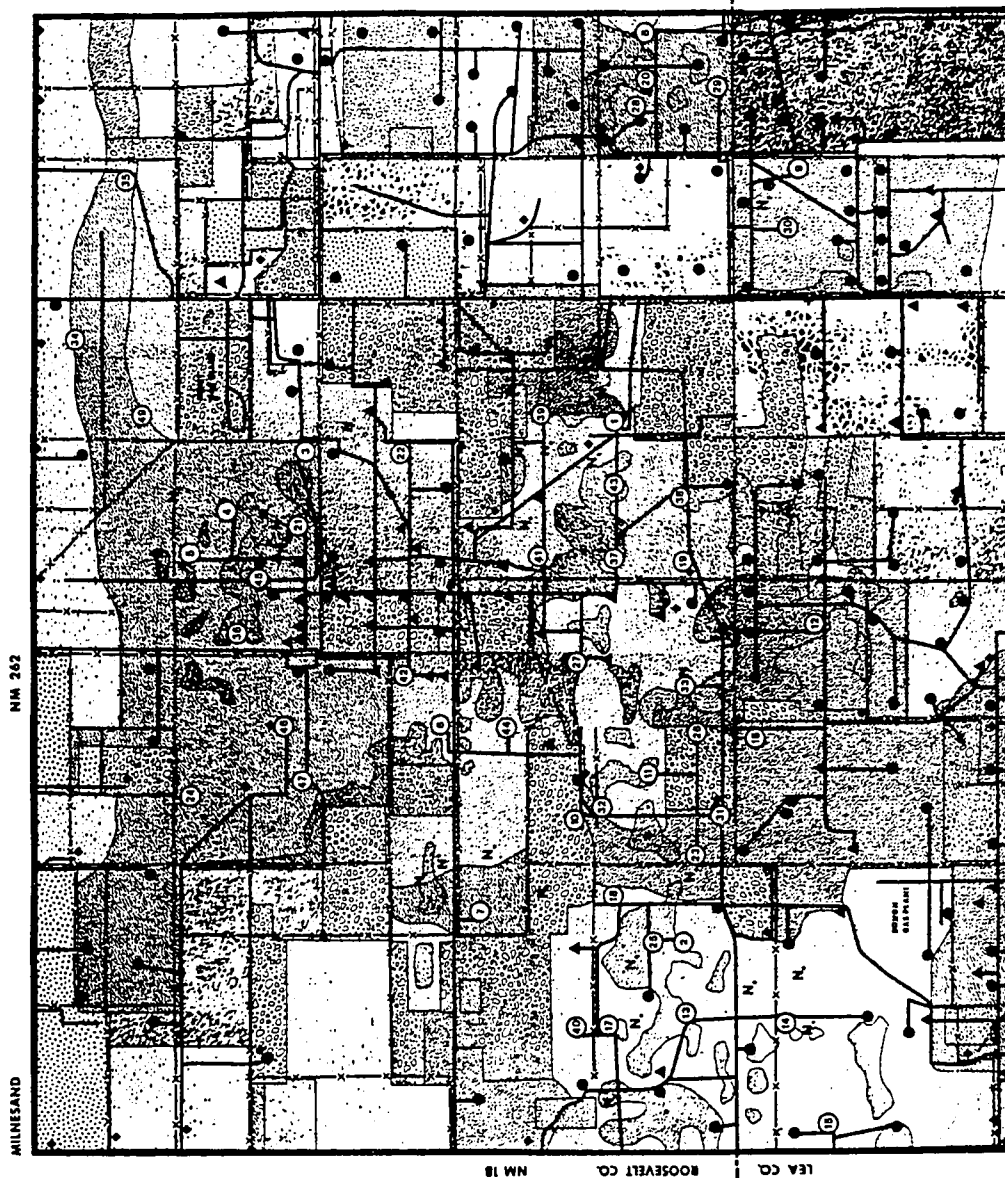
### Leks and Display Sites

Twenty-one leks were located in 1983. Nineteen of the 21 leks occurred on oilpads, the other 2 were in naturally occurring vegetation. Thirty four leks were located in 1984, only 3 of which were located in naturally occurring vegetation.

Many unused oilpads were available for use by displaying males. In 1983 only 21 of 48 oilpads in the area sampled were used for leks, and in 1984 only 34 of 67 oilpads were utilized as display sites. The oilpads are apparently preferred as display sites over the natural vegetation, but oilpads are not a limiting resource on the study area. It is clear that males are not clumped for lack of suitable display sites.

Table 1 lists the number of leks and unused oilpads found in each of the vegetative cover types. Many

**Figure 2.** Map of study area (from Davis et al. 1982).



SHINNEY OAK-BLUESTEM  
 SHINNEY OAK-MIDGRASS  
 SHORTGRASS-SNAKEWEED  
 REVERTED CROPLAND  
 WEEPING LOVEGRASS  
 CULTIVATED  
 SANDHILLS  
 FALLOW

FENCES  
 ROADS  
 N. NESTS  
 L. LEXS  
 WATERS  
 INACTIVE PETROLEUM SITES  
 ACTIVE PETROLEUM SITES

1.0 km  
 N

**Table 1.** Leks and unused oilpads by adjacent vegetative cover.

<u>Cover types</u>	<u>1983<sup>a</sup></u>		<u>1984<sup>b</sup></u>	
	<u>Leks</u>	<u>Unused</u>	<u>Leks</u>	<u>Unused</u>
Sandhills	8	2	11	5
Shinnery oak-bluestem	5	15	13	10
Shinnery oak-midgrass	7	2	9	8
Reverted cropland	1	5	0	6
<u>Other</u>	0	3	0	4

<sup>a</sup> G test of independence significant ( $P < 0.05$ ) for sandhills and shinnery oak-midgrass versus shinnery oak-bluestem.

<sup>b</sup> G test of independence not significant ( $P > 0.05$ ) for any of the three shinnery oak dominated cover types.

oilpads were available in each of the cover types. In 1983 20 of 21 leks found were located in the shinnery oak-dominated cover types, and 19 unused oilpads were available in those same cover types. Results for 1984 were similar. Most of the same oilpads were utilized for lekking two years in a row, and there were no major disturbances to alter vegetative cover on the study area.

There was no association between oilpads used for leks and adjacent cover types. A G-test of independence (Sokal and Rohlf 1981) was used to determine if the data listed in Table 1 indicate that oilpads adjacent to one cover type might be more likely to be used than oilpads adjacent to

other cover types. There was no association between either of the three shinnery oak cover types and the proportion of oilpads occupied by leks in 1984 ( $P > 0.05$ ). The numbers of unused pads in sandhills and shinnery oak-midgrass cover types were too small to be tested, and were combined for 1983 (Sokal and Rohlf 1981). The proportion of pads used for lekking in shinnery oak-bluestem habitat was significantly lower than the proportion of oilpads used for lekking in the sandhill and shinnery oak-midgrass cover types combined ( $P < 0.05$ ). This statistical result is probably due to some factor other than the cover type surrounding the lek. The 1984 data include all of the area sampled in 1983, plus some additional area. The number of unused oilpads decreased from 15 in 1983 to 10 in 1984. Some of the oilpads adjacent to shinnery oak-bluestem cover that were not used in 1983 were used in 1984, indicating that they were suitable display sites.

Seventeen new leks were formed between 1980 and 1984. The location of those leks in relation to vegetation types and existing leks should help elucidate factors important to the formation of leks. Table 2 lists these new leks. They fall into two groups: 1) spring leks that existed in 1983 or 1984, but formed after 1980; and 2) spring leks known to exist first in 1984.

**Table 2.** Establishment and relative position of new leks formed since 1980.

Lek	Closest Lek	Closest Pad?	Habitat	Year Established
31	11	no	rc <sup>a</sup>	1980<?<1983
32	11	yes	sh <sup>b</sup>	1980<?<1983
34	4	no	mg <sup>c</sup>	1980<?<1983
35	3	no	bs <sup>d</sup>	1980<?<1983
36	5	no	sh	1980<?<1983
37	27	yes	sh	1980<?<1983
38	19	no	bs	1980<?<1983
39	1	no	sh	1980<?<1983
40	17	yes	bs	1980<?<1983
46	24	no	mg	1980<?<1983
47	24	no	mg	1980<?<1983
41	27	yes	bs	1984
42	6	no	bs	1984
43	1	yes	sh	1984
44	6	no	bs	1984
45	5	yes	sh	1984
49	4	no	bs	1984

<sup>a</sup>rc = reverted cropland

<sup>b</sup>sh = sandhills

<sup>c</sup>mg = shinnery oak-midgrass

<sup>d</sup>bs = shinnery oak-bluestem

If leks were located near a specific foraging area, or some other form of hotspot (Lill 1974b), then any new leks should be located on the closest available oilpad. However, of the 13 new leks that occurred on oilpads, only 5 occurred at the oilpad closest to an already existing lek.

I compared the habitat that the new leks were found in with the habitat surrounding the pads nearest to the existing leks. A two-way test of independence was not significant ( $P > 0.05$ ), suggesting no preference. Because



of small frequencies, the shinnery-oak bluestem, shinnery-oak midgrass, and reverted cropland vegetation types were combined into one vegetation type. The other vegetation type was the sandhills type. Failure to use the nearest oilpad as a new lek site was not due to the nearest pads occurring in vegetative types different from those in which already existing leks occurred.

#### **Number of Males per Lek**

Table 3 lists the average number of males displaying on leks that were surveyed in both 1983 and 1984. A comparison of the average number of males per lek between years, using only leks in areas surveyed in both 1983 and 1984, is insignificant ( $t = 0.98$ ,  $P > 0.05$ ). There was not a significant change in the average number of males per lek between 1983 and 1984.

The number of males per lek was not associated with the amount of vegetative cover on the oilpad on which the lek was located. A Spearman's rank correlation of 0.66 ( $P < .01$ ) was found to exist between the number of males per lek and the vegetative cover on 18 of the oilpads on which leks occurred on in 1983. A Spearman's rank correlation of only 0.21 ( $P > 0.05$ ) was found between the number of males per lek and the vegetative cover on those same 18 oilpads in 1984. Many of the newer leks formed on oilpads without any vegetative cover. Lek 7 occurred on one of the oilpads

**Table 3.** Average number of males displaying on leks located in areas surveyed in both 1983 and 1984.

LEK	$\bar{X}$ Males	1983			$\bar{X}$ Males	1984		
		Visits Total <sup>a</sup>	AM <sup>b</sup>	SD <sup>c</sup>		Visits Total	AM	SD
1	15.0	4	3	2.6	16.8	5	5	3.0
3	28.0	2	1	-	22.5	3	2	-
4	8.5	2	2	2.1	4.0	3	1	-
5	21.5	2	2	0.7	14.3	3	3	3.8
6	17.5	4	2	3.5	16.4	11	11	1.9
7	24.5	4	2	4.9	9.2	6	5	5.8
11	8.6	12	8	2.5	14.3	7	6	2.3
16	18.0	4	3	2.4	13.3	5	3	4.0
19	17.4	7	6	4.7	19.1	14	10	4.7
22	14.0	6	4	2.9	14.0	8	7	5.8
23	10.3	7	4	3.1	6.8	6	4	2.1
26	4.0	7	5	1.0	0.0	7	2	-
27	8.3	8	4	1.5	11.0	6	4	0.8
31	10.4	9	5	4.3	12.4	8	7	4.1
32	3.0	3	2	0.7	7.3	7	4	1.7
33	4.0	2	1	-	0.0	4	2	-
34	11.3	6	3	2.8	6.0	4	2	1.4
35	10.0	5	1	-	15.0	4	1	-
36	10.0	5	1	-	9.0	3	1	-
37	5.0	7	1	-	6.8	9	4	0.5
38	0.0	9	5	-	2.0	9	1	-
39	5.0	9	1	-	5.3	7	4	1.3
41	0.0	8	4	-	6.0	4	4	2.2
42	0.0	2	2	-	5.5	4	3	1.7
43	0.0	7	5	-	7.3	3	3	1.2
44	0.0	2	2	-	9.5	2	2	4.9
45	0.0	2	2	-	9.0	3	3	2.6
49	0.0	6	3	-	9.0	3	1	-

Leks	21	26
Males	254.3	271.8
Mean	12.1	10.5 <sup>d</sup>
Std. Dev.	7.0	5.0

<sup>a</sup> Total attempts to verify lek existed.

<sup>b</sup> Early AM counts to determine number of males using lek.

<sup>c</sup> Standard deviation of mean number of displaying males.

<sup>d</sup> Means not different,  $t = 0.95$ ,  $P > 0.05$ .

with the most vegetative cover. The average number of males in lek 7 was very high in 1983, 24.5, but only 9.2 in 1984. Clearly the amount of vegetative cover on the oilpad itself does not control the number of males that will lek at that oilpad.

The average number of males in a lek was not correlated with the amount of any of the different vegetation cover types surrounding the lek. Table 4 lists the correlations between the number of males on the lek, and the amount of each of four vegetative cover types within a 122-ha circle centered on the lek. The size of the circle is based on the average female home range measured by Merchant (1982) for 1980.

**Table 4.** Pearson product-moment correlations between number of males per lek and amounts of each vegetative cover type in 122 ha circle centered on lek.

<u>year</u>	<u>sandhill</u>	<u>shinnery-oak bluestem</u>	<u>shinnery-oak midgrass</u>	<u>reverted cropland</u>
	<u>r</u>	<u>r</u>	<u>r</u>	<u>r</u>
1983	-0.43	0.09	0.11	0.18
1984	-0.18	0.20	-0.19	-0.16

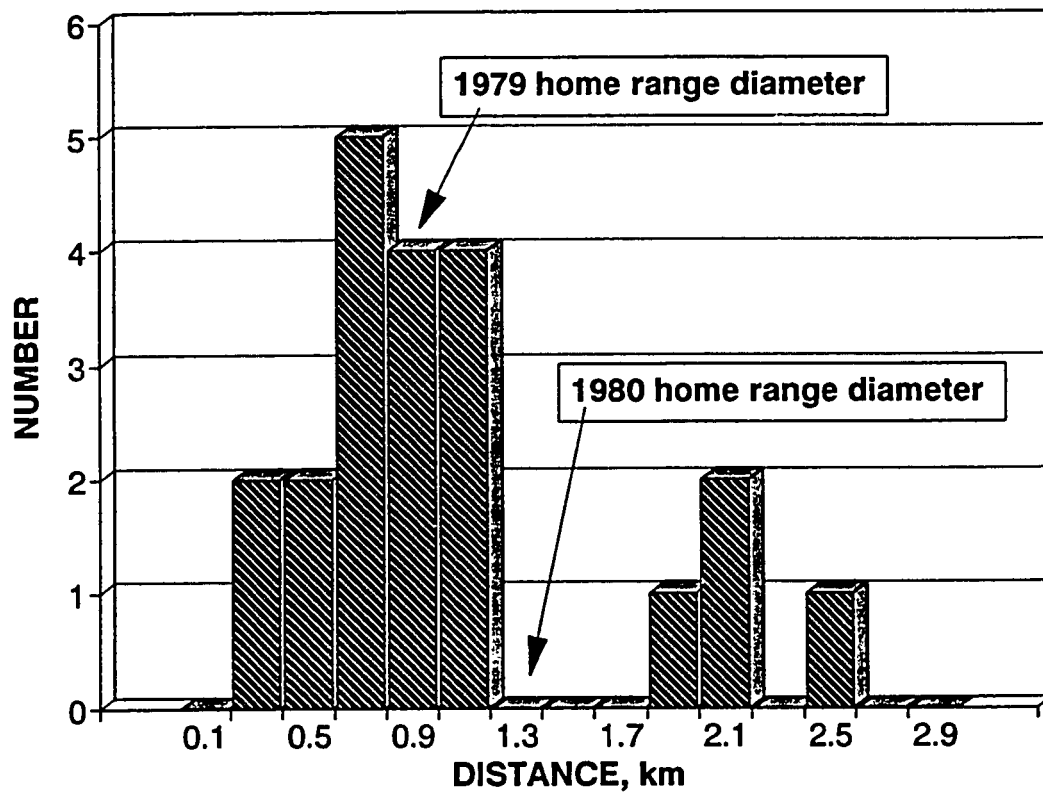
#### Distance Between Leks

Less than half of the leks located in 1983 were as far apart as the female preference model predicts (Bradbury 1981). The distribution of distances between leks located

in 1983 is shown in Figure 3. Female home ranges were measured by Merchant (1982) on this same study area, and are used in this comparison. Merchant (1982) reported home ranges of 62.7 ha for 1979, and 121.8 ha for 1980. These female home range estimates reported by Merchant (1982) are at the lower end of the 62 to 300 ha range reported for female Lesser Prairie Chickens in Bradbury et al.'s (1986) review. As minimal estimates of home range size, these estimates are conservative in terms of testing the female preference model.

The diameter for a circular female home range of the size measured by Merchant (1982) during the pre-nesting season was 893 m in 1979, and 1245 m during 1980. Eleven of the 21 leks located in 1983, 52 %, were as close or closer to another lek than the diameter of the 1979 female home range. Seventeen of 21, 81 %, of the leks located in 1983 were closer to another lek than the diameter of the 1980 average female home range.

Figure 4 shows the distribution of distances between each lek and the lek closest to it for leks located in 1984. There was an increase from 21 to 34 leks, with a small increase in the area sampled. A net increase of 5 leks occurred over the area sampled both years. At least 25 of 34, 74 %, of the leks located in 1984 were closer to another lek than the female preference model suggests. At



**Figure 3.** Distribution of distances between adjacent leks in 1983. Female home range data from Merchant (1982).

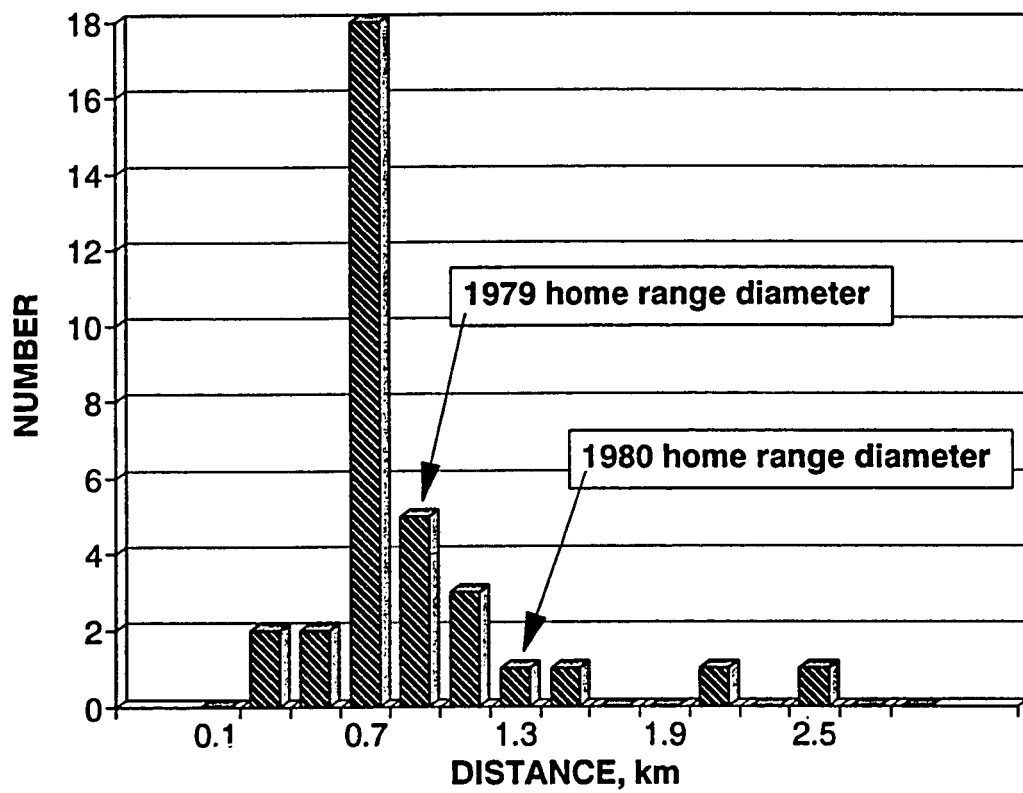
least 31 of 34, 91 percent, of the leks located in 1984 were closer to another lek than the diameter of the 1980 average female home range. Most of the leks located in 1983 and 1984 were closer to another lek than the diameter of an average female home range measured on the study area by Merchant (1982). These results contradict the female preference model, even before considering the distance at which a lek could be detected by females.

#### **Detection Distance**

Bradbury (1981) mentioned that the distance at which a lek can be detected is rarely determined or reported. This distance is important because the female preference model predicts that the distance between adjacent leks is not larger than one female home range diameter plus twice the distance at which a lek can be detected. The following observations suggest that leks can be detected at least 0.7 km away.

On 22 March 1983 I saw a group of 11 birds join lek 31. A female was present at lek 31. Fourteen birds then left lek 31 and flew to lek 16, 0.91 km away. Water was present at lek 31, but only a few of the visiting males drank.

On 17 March 1984 I discovered 27 birds at what became lek 42, 0.71 km NE of lek 6. I had recently checked the lek 6 location and found no birds there. Only 6 birds could be seen on the oilpad, the other 21 birds were in the



**Figure 4.** Distribution of distances between leks in 1984. Female home range data from Merchant (1982).

tall shinnery oak near the oilpad. Not seeing the birds hidden by the shinney oak, I flushed the other birds before determining if a female was present. The birds flew directly towards the lek 6 oilpad, 0.71 km away. I located the lek 42 birds by listening, I first heard the calls from the lek 6 location. The males were calling as if a female was present. There was no free water available at or near the oilpads utilized by leks 42 or 6.

On three separate days I observed males referred to as lek 19, moving back and forth between their normal display ground, and a puddle of water where a female had apparently come to drink. Males were already displaying to the females when large portions of the males in attendance at lek 19 would move to the water puddle area and begin displaying. The distance to the water puddle was only 100 m or so, but that enabled me to determine, by sight, that at least one female was at the water puddle each time a group of males moved to the water puddle. A group of males moved between display sites at least three times on each of the three days this behavior was observed. It appeared that these were largely the same individuals moving to the water puddle and back, based on their relative display positions at lek 19.

Water was available in all but one of the movements cited above. However, the water appeared to served mainly



to attract a female, strictly as a localized hotspot. The majority of males did not drink at the water puddles during these observations. I never saw the lek 19 males move to the nearby water puddle unless a female was already present.

These observations of leks moving are valid in establishing a minimum distance at which Lesser Prairie Chickens can detect the presence of a lek. This behavior of males moving to adjacent display sites is sometimes paralleled by male movements within leks. I have seen males fly from one end of a lek to another, in an apparent attempt to get females to fly off the lek. The resource males were seeking in their movements were females, not water.

Males abandoning established territories during display periods has also been observed in other lekking species (Gibson and Bradbury 1987). Gibson and Bradbury (1987) interpreted the male movements as a strategy to enhance probability of obtaining a mate.

#### **Interruption of Copulation Attempts with Female Model**

The hotshot hypothesis explains leks by postulating that females do not have total freedom in choosing mates. Male dominance and female choice produce a skew in mating success. Males congregate around certain other males that

are more successful in attracting females (Beehler and Foster 1988).

Beehler and Foster (1988) suggest that hotshot males will exert dominance over less successful males, and that male-male interactions influence female choice. Male-male interactions may cause females to exercise mate choice in a manner that will minimize the chance of interruption of copulation attempts, and, or danger to the female. Such male-male interactions are described in this summary of observations of males' behavior towards a female taxidermic model in copulatory position.

Males made initial attempts to copulate on 6 of 12 opportunities. Ejaculate was observed on the taxidermic mount only once. The taxidermic mount was capable of eliciting copulatory behavior in males.

Males failed to attempt to copulate with the model on 6 different occasions. On 4 of those 6 occasions the male normally in that location of the lek was not present. On 3 of these 6 occasions the males in the center of the lek were not present. On both of the occasions in which the territory owner was present, but no copulation attempts were made, the territory owner had previously attempted to copulate with the model. In both of those cases the territory owner was captured in carpet nooses after the copulation attempt.

Copulation attempts were interrupted on 3 of the 6 copulation attempts. Females were present in a different portion of the lek during one of the cases in which a copulation attempt with the model was not interrupted. Both of the males that were not interrupted were in locations females had visited either before or during the observation period. Two of the three males interrupted were adults, the other a juvenile. In one instance an adult male did not attempt to copulate with the model until after two other males near the model were caught in noose carpets, and obviously distracted.

These observations illustrate the type of male-male interactions predicted by the Hotshot model (Beehler and Foster 1988). In one of the interruptions, one of the interfering males directly attacked the female mount. Beehler and Foster (1988) point out that females may behave in such a way that male influence of female choice may be hard to observe.

## DISCUSSION

### Female Preference Model

The maximum distance at which a lek can be detected by females would have to be quite short for the female preference model to fit observations on the distances between leks. A female home range of only 62 ha (smallest female Lesser Prairie Chicken home range reported by Merchant 1982 and Bradbury et al. 1986) requires a detection range of only 64 m to fit the female preference model, and the average distance between leks found in 1983 (1.02 km). The detection range would have to be even smaller to fit the average distance between leks observed in 1984 (0.84 km).

Observations suggest that the distance at which females can detect leks is much greater than the 64 to 228 m required for the female preference model to fit the different studies at the Milnesand area. Oring (1982) suggested that birds could likely detect leks at similar distances to humans. Svedarsky (1988) felt that the distance of detection of Greater Prairie Chickens was as great as 3 km. My observations of males moving temporarily off of leks to approach females suggests that Lesser Prairie Chickens can detect leks from at least 0.7 km away. I have heard leks from as far away as 2.3 km.

Male vocal calls can act as a mechanism for males to determine if males are displaying to females. I found that the intensity of display, and pitch of calls can be used to indicate that males are displaying to females. Studies of Greater Prairie Chickens have described a "Whoop Call," which functions as a way to inform birds "quite far away" that a female is attending a lek (Hjorth 1970). Hamerstrom and Hamerstrom (1960) mentioned that "Whooping is only done consistently in the presence of females."

The female preference model suggests two manners in which the abundance of males should increase in a fixed area. Increases in male abundance would be accompanied by increases in the average number of males per lek, or new leks would form more than one female home range diameter away from existing leks. Changes in abundance of displaying male Lesser Prairie Chickens is accompanied by increases in the number of leks, rather than significant differences in the average number of males per lek (Cannon and Knopf 1981, Merchant 1982, this study). However, 9 of 17 new leks formed at the Milnesand area since 1980 occurred at locations within a female home range diameter (893 m) of existing leks. As the population grew, the distance between leks decreased. Eight of those 9 leks could have been placed on oilpads further away from existing leks.

Predictions of the female preference model do not fit the dispersion of leks in the Lesser Prairie Chickens. One reason the leks may be so close together is the relative homogeneity of vegetation on the study area. I found no correlations between vegetative cover types and where leks were located, or the number of males on the lek. Similarly, Merchant (1982) found no vegetative preference for females during the pre-nesting period. Höglund and Robertson (1990a) report that Great Snipe leks were spaced in accordance with the female preference model, but their study area has a heterogenous mix of vegetative cover types and they report that the Great Snipe prefers a particular type for display. Höglund and Robertson (1990a) refuted the female preference model because most females attended more than one lek, a contradiction of the model. Schroeder (1991) reported that most female Greater Prairie Chickens visited more than one lek, and that leks were too close together to fit the female preference model. The female preference model does not fit lek dispersion distances for the Greater Prairie Chicken (Svedarsky 1988), nor the Black Grouse (Wegge and Rolstad 1986).

#### **Hotspot Model**

The hotspot model (Bradbury and Gibson 1983) allows leks to be closer together, or farther apart, than the female preference model. An increase in the density of

females would allow a decreased mean distance between leks (Bradbury et al. 1986). The decreased distance between leks coupled with increases in displaying males observed by both myself, from 1983 to 1984, and by Merchant (1982) in 1979 to 1980, may indicate that the number of females increased also. Assuming that female densities increased with male densities, the increase in the number of leks and the decrease in distances between leks are in agreement with the hotspot model (Bradbury et al. 1986).

#### **Lack of Suitable Display Sites**

Another reason for lekking might be lack of suitable display sites (Bradbury and Gibson 1983). Males at Milnesand did not congregate and form leks because of a lack of suitable display locations. A preference for oilpads in shinnery-oak habitats is obvious (Ahlborn 1980, Davis et al. 1982), but many oilpads were unused for lekking. Some oilpads not used in 1983 were apparently suitable as display sites, as they were used in 1984.

#### **Decoy/Sentinel Model**

The decoy/sentinel model suggests that females can encourage males to aggregate their display areas and form leks (Phillips 1990). The main prediction of this model is that nesting success will vary with distance from the lek. Specifically, successful nests as a group should show less variation in distance away from the nearest lek than will

unsuccessful nests. Nests found at the Milnesand area by Davis et al. (1982) in 1979 do not fit the prediction, the variability in distance to the nearest lek was not statistically different between successful and unsuccessful nests (F-test,  $P < 0.05$ ). Merchant (1982) did not find any successful nests in 1980, and attributed the lack of nesting success to an abnormally dry year. Combining 1979 and 1980 nest data yields an agreement with the decoy/sentinel idea, but there is no way of knowing whether the nests were abandoned before the nest was discovered by predators, or afterwards.

Davis et al. (1982) used cannon nets to capture birds on the leks. Phillips (1990) declined to use data sets when cannon nets were used at the lek because they may disrupt male display and diminish the function of males as decoys or sentinels. Phillips (1990) mentions that Svedarsky (1969) reported the use of cannon nets disrupted male display. However, there is no evidence that the use of cannon nets by Davis et al. (1982) disrupted male display. This may be because the use of cannon nets was spread over 5 different leks. Of 15 nests found in 1979, only 5 were closest to a lek that was used to capture females. Three of these 5 nests were unsuccessful. None of the nests located by Davis et al. in 1980 were located nearest a lek that was used to capture females with a



cannon net. Furthermore, the average distance between nests and the nearest lek for nests found by Davis et al. (1982) was not statistically different than the value reported for another Lesser Prairie Chicken study in which a cannon net was not used (Davis et al. 1981, in Phillips 1990).

The decoy/sentinel idea seems reasonable if by mate choice females can keep leks from forming in the zone of fewer predators. Successful nests located by Davis et al. (1982) averaged 610 m away from the nearest lek. Phillips (1990) reports that successful nests located at the Chaves Co. study area by Davis et al. (1981) average about 664 m from leks. Adjacent leks should be a minimum of twice the average distance between nests and the closest leks. If closer, the zone of fewer predators postulated to occur around each lek will overlap with the zone of higher predator density of the lek too close.

Females at Milnesand were not able to force leks to spread out in order for male presence to decoy predators near the lek and away from nests. The greatest average distance between adjacent leks was 1.35 km in 1979, and over half of the leks were closer to another lek than the minimum of at least 1220 m. In 1980 the average distance between leks was 1020 m. Most leks are close enough to other leks to decoy predators into the zone of fewer

predators of the other lek. The potential benefit, to nesting females, of possibly attracting predators to leks is easy to understand. However, the benefit of leks as decoys appears to be a consequence of leks rather than a mechanism for their evolution since females do not appear to be able to control where leks are placed.

#### **Least-Costly Male**

The least costly male hypothesis (Wrangham 1980) is another female-initiated hypothesis. Females avoid displaying males because they may compete for food, and, or attract potential nest predators. Bergerud (1988) claims that female grouse avoid leks and that the average difference between nests is about one-half the average distance between leks. Unpublished data of Davis et al. (1982) do show that the average distance between nests and the nearest leks in 1979 (617 m) was about half of the average distance between adjacent leks (1.35 m). However, increases in both the number of leks, and the number of males on the Milnesand study area led to an average distance between adjacent leks of only 840 m in 1984. As discussed for the decoy/sentinel idea, females do not seem to be able to keep males from creating new leks that decrease the average distance between leks. Nest predation is relatively high in many ground-nesting birds (Lack 1968), but lekking is not common in such birds.

In support of the least-costly male hypothesis, Bergerud (1988) suggests that the large pre-nesting home ranges seen in lekking grouse (Bradbury and Gibson 1983) are part of a female strategy for avoiding predation. Bergerud reasons that since the ranges of hens during the nesting season are much smaller, lack of food does not cause the pre-nesting ranges to be as large as observed. However, Merchant (1982) attributed an average prelaying home range that was double the previous year (1979 vs. 1980) to low rainfall and its effect on food availability. Davis et al. (1982) noticed that copulation and nesting in Lesser Prairie Chickens seem to arrive with late spring green-up. The availability of food is apparently low until the shinnery oak produces catkins in the spring. Davis et al. (1982) noted that most of their birds migrate to agricultural areas until spring leks began to form. As Wittenberger (1978) and Bradbury (1981) point out, food may be the cause of the large female home ranges in lekking grouse.

#### **Hotshot Hypothesis**

The hotshot model (Beehler and Foster 1988) suggests that less successful males display around males successful in obtaining mates, the "hotshots." Beehler and Foster (1988) suggest that female mate choice does occur, but that such choice is not as free or as important as previously

believed (Bradbury 1981, Bradbury and Gibson 1983, Bradbury et al. 1985). Beehler and Foster (1988) suggest that male-male interactions such as interference with copulations may constrain female choice and lead to the high degree of skew in male mating success of lek species. I found disruptions of attempted matings to occur on 3 of 6 attempts at mating with a female taxidermic mount in a copulatory position. Furthermore, on 6 opportunities males did not mount the taxidermic mount even though they displayed to it for some time. Apparently males may be reluctant to mount a female and incur a fight. Male-male interactions may be important in mate choice, especially if they keep males from entering the competition (Foster 1983, Beehler and Foster 1988, Höglund and Robertson 1990b).

The form of dominance interaction between males may be subtle (Beehler and Foster 1988). Females may exercise mate choice in a manner that minimizes the chance of interruption, thus reducing the opportunity for field workers to observe interruptions. Such choices by females may be immediately rewarded if females were in danger when they made a poor choice. One of the males that interrupted an attempted copulation with a taxidermic mount also directly attacked the taxidermic mount itself.

## CONCLUSIONS

Lek spacings of the Lesser Prairie Chicken were inconsistent with the female preference model, least-costly male hypothesis, and the decoy/sentinel model. Unpublished data on nest success from Davis et al. (1982) also contradict predictions of the decoy/sentinel model.

Display sites were not a limiting resource, and can not explain why males lek. Portions of the study area used by Lesser Prairie Chickens are relatively homogeneous, and within those areas, recognizable vegetative types do not explain differences in numbers of males between leks, nor why some oilpads were used for lekking sites and others were not.

Lesser Prairie Chicken populations tend to enlarge by increasing the number of leks rather than increasing the number of males per lek (Cannon and Knopf 1981, Merchant 1982, this study). Adding new leks in a fixed area decreases distances between leks. This negative relationship between population density and distance between leks is a prediction of the hotspot hypothesis.

The wide variation in numbers of males attending leks conforms to predictions of the hotshot hypothesis. Dominance of males over others also appears to occur, as some males would not attempt to mount a taxidermic model, even though they had no previous experience with the model.

Other males were attacked immediately upon mounting the model.

Most of the hypotheses to explain the evolution of leks are not mutually exclusive (Oring 1982), several factors may work together to produce the patterns observed (Bradbury et al. 1989b, Gosling and Petrie 1990, Höglund and Robertson 1990a, Schroeder 1991). Both the hotspot and hotshot hypotheses seem to apply to lekking in the Lesser Prairie Chicken.

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